Weed Science 2007 55:123–128

Nitrogen Fertilizer and Crop Residue Effects on Seed Mortality and Germination of Eight Annual Weed Species

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Weed seed persistence in the soil seedbank is central to weed population dynamics; however, limited knowledge of mechanisms regulating seed survival in soil remains an obstacle to developing seed-bank management practices. Weed seeds are rich in carbon and nitrogen, and therefore may represent an important nutritional resource to soil microbes. The objective of this study was to test the hypothesis that weed seed mortality due to microbial predation is limited by soil inorganic N availability and soil C:N ratio. A factorial of N fertilizer rate (0, 14, and 28 mg N kg soil^{-1}) and corn stover addition rate (0 and 3,000 mg stover kg soil^{-1}) was applied to bioassay units containing Illinois field soil (silt loam, 3.8% organic carbon) and seeds of one of eight annual weed species common to Illinois field crops: giant foxtail, green foxtail, yellow foxtail, wooly cupgrass, giant ragweed, redroot pigweed, velvetleaf, and Venice mallow. Seeds were incubated for 2 mo, after which they were recovered from the soil and tested for viability. Only three of the eight species, velvetleaf, giant ragweed, and wooly cupgrass, responded to the experimental treatments. Velvetleaf seed mortality was 40% lower in the corn stover–amended treatment than in the unamended treatment. Both giant ragweed and wooly cupgrass showed a more complex interaction between N fertilizer and corn stover treatments. Path analysis supported the hypothesis that the influence of soil N on seed mortality in velvetleaf was because of the direct effect of soil N on microbial predation of velvetleaf seeds, whereas for giant ragweed and wooly cupgrass, the effect on seed mortality appeared to be mediated through soil N effects on germination. Mechanisms underlying soil N fertility effects on weed seed mortality appear to be species-specific. Future investigations of this phenomenon should include quantitative measures of seed coat composition and quality.

Nomenclature: Giant foxtail, *Setaria faberi* Herrm. SETFA; giant ragweed, *Ambrosia trifida* L. AMBTR; green foxtail, *Setaria viridis* (L.) Beauv. SETVI; redroot pigweed, *Amaranthus retroflexus* L. AMARE; velvetleaf, *Abutilon theophrasti* Medik. ABUTH; Venice mallow, *Hibiscus trionum* L. HIBTR; wooly cupgrass, *Eriochloa villosa* (Thunb.) Kunth ERIVI; yellow foxtail, *Setaria glauca* (L.) Beauv. SETLU.

Key words: Seed mortality, soil carbon and nitrogen, C:N ratio, N fertilizer, microbial degradation, germination, organic amendment, weed seedbank management.

Weed seed persistence in soil seedbanks is thought to be determined by a combination of factors, including heritable traits, the maternal environment in which a seed develops, and soil biological, chemical, and physical properties (Gallagher and Fuerst 2005). Producers have little control over the genetics of weed populations, a moderate amount of control over the maternal environment of seeds, and a good deal of control over certain soil properties, such as fertility, soil organic matter content, and structure (Brady and Weil 1996). Therefore, it may be useful to approach weed seed-bank management with the goal of manipulating soil properties to favor weed seed mortality (Chee-Sanford et al. 2006; Gallandt et al. 1999). Soil moisture (Mickelson and Grey 2006; Schafer and Kotanen 2003) and temperature (Davis et al. 2005), seed burial depth (Benvenuti et al. 2001), and management-related variation in soil microbial community (Davis et al. 2006) have all been found to influence weed seed-bank persistence.

Producers routinely alter soil C and N dynamics through N fertilization and plant residue management (Fortuna et al. 2003; Marriot and Wander 2006). Residue quality, often understood through C:N ratios, is an important driver of the decay of organic materials (Jensen et al. 2005). Weed seeds may serve as a nutritional resource to soil microbes, but the high C:N ratio of the seed coats of many weed species (Chee-Sanford et al. 2006) may deter rapid deterioration of the seed. If such a barrier exists, could enrichment of soil N with fertilizer applications remove nutrient limitations to microbial degradation of seeds? Soil inorganic N, especially in the form of NO_3–N, is also known to stimulate the germination of many weed seeds (Egley 1986; Benech-Arnold et al. 2000). Thus, for those species using N as a signal for germination, N fertilizer additions could potentially limit seed mortality by increasing germination, which leaves fewer seeds exposed to the soil microbial community.

A previous study (Shem-Tov et al. 2005) showed that seed viability of burning nettle (*Urtica urens* L.) decreased when incubated in soil with C:N ratios less than 25:1, compared to soils with greater C:N ratios. The objective of the present study was to extend these findings to weed species commonly found in field crops of the north-central region of the United States while limiting C and N inputs to soil to within agronomic levels. Two alternate hypotheses were investigated here: that additions of crop residue and fertilizer N to soil will influence soil fertility parameters and thereby affect weed seed mortality either (1) indirectly, by altering seed germination patterns and overall seed fate (i.e., more germination, less mortality), or (2) directly, by stimulating or inhibiting microbial predation of weed seeds.

Materials and Methods

Hypotheses 1 and 2 were addressed by conducting bioassays of the effect of soil amendment with N fertilizer and corn stover on seed mortality of eight summer annual weed species. Bioassays were performed in a randomized complete block design with four replications of a factorial of species, N fertilizer rate, and corn stover amendment rate.

The study species included four forbs (giant ragweed, redroot pigweed, velvetleaf, and Venice mallow) and four grasses (giant foxtail, green foxtail, yellow foxtail, and wooly

DOI: 10.1614/WS-06-133.1

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cupgrass) common to corn and soybean production systems in central Illinois. These species spanned a wide range in seed size, with an 80-fold difference in seed mass between the largest seeds (giant ragweed, 2.958 g 100 seed^{-1}) and the smallest seeds (redroot pigweed, 0.037 g 100 seed^{-1}). Weed seeds of the eight species included in this investigation were harvested from residual stands within experimental plots at the University of Illinois Crop Sciences Research and Education Center (CSREC) in Urbana, IL, in fall of 2004. Seeds were hand-harvested by gently shaking mature seed heads over a container. Light seeds and chaff were removed with a seed cleaner,[1] and remaining seeds were placed in airtight plastic bottles and stored at 4 C until ready for use. One week prior to the initiation of the bioassays, each of the seed lots was subjected to tetrazolium testing (Peters 2000) to determine initial percentage of seed viability.

Soil amendment treatments consisted of a factorial of three rates of urea ammonium nitrate (28% UAN) fertilizer addition (0, 14, and 28 mg N kg soil^{-1}) and two rates of ground corn stover addition (0 and 3,000 mg stover kg soil^{-1}). The 0, 14, and 28 ppmw N application levels corresponded approximately to field application rates of 0, 28, and 56 kg N ha^{-1}, respectively, calculated on the basis of a 1-ha area of soil 15 cm deep with an average bulk density of 1.33 g cm^{-3} soil. The 0 and 3,000 ppmw corn stover rates corresponded to 0 and 6,000 kg stover ha^{-1}, again using the volume-based calculation method described above. Corn stover amendment rate was based on the average post-harvest biomass of corn stover found on the soil surface of several field plots located at CSREC. Corn stover was collected 2 wk after corn harvest and then dried to constant weight before being ground on a Wiley mill[2] and stored in an airtight plastic container prior to use. Although this process produced finer particles than would be observed initially after harvest under field conditions, the decision to grind residue was made to ensure even distribution of residue in mixture with soil, thereby reducing spatial heterogeneity.

Experimental units consisted of 5-cm-diam by 5-cm-deep plastic cups containing a standard number of seeds (25 seeds per experimental unit for giant ragweed, velvetleaf, and wooly cupgrass; 50 seeds per cup for all other species) planted 2.5 cm deep in 80 g of soil. The soil collected at CSREC was a Raub silt loam (Aquic Argiudoll, 28% sand, 62% silt, 10% clay, and 3.8 % soil organic carbon and pH 6.5). Initial soil moisture was 26.5%, corresponding to a matric potential of −33 kPa, or approximately field capacity. Soil C:N ratios and soil total inorganic N (NO_3–N + NH_4–N) at 1 wk after the initiation of the bioassay were determined with a CHN analyzer[3] and accelerated diffusion methods (Khan et al. 1997), respectively. Ambient viable seedbank densities for target species in the study soil were determined through elutriation (Wiles et al. 1996) followed by tetrazolium testing.

Two runs of the bioassay were performed in a Conviron 125L incubator,[4] with a 2-wk offset in starting time between the first and second runs. The incubator was programmed to deliver a diurnal cycle of 12 h dark at 15 C and 12 h light at 25 C, with a photosynthetic photon flux density of 40 μmol m^{-2} s^{-1}. Experimental units were placed inside transparent plastic bins to minimize moisture loss. The starting weight of each experimental unit was recorded, and water was added as necessary to replace moisture losses detected by daily weighing. Emerged seedlings were counted and plucked weekly, taking care to remove the growing point of the seedling with as little soil disturbance as possible. After a 2-mo incubation period, each experimental unit was elutriated and then dried at 35 C for 24 h. Remaining seeds were counted and characterized as viable or nonviable using tetrazolium assays. Percentage of weed seed mortality (μ) in bioassays was calculated using Equation 1

$$\mu = \frac{(s_0 + a_0) - (s_1 + g)}{(s_0 + a_0)} \times 100\% \qquad [1]$$

where s_0 = the number of viable seeds added at the start of the bioassay, a_0 = the estimated number of ambient seeds present in the study soils at the start of the bioassay, s_1 = the number of viable seeds recovered at the end of the assay, and g = the number of emerged seedlings. Estimates of seed mortality did not distinguish between seed mortality because of fatal germination or seed mortality because of microbial decay.

Nitrogen fertilizer and corn stover effects on the activity of the soil microbial community itself were not measured in this experiment. The reasoning behind this decision was that microbial involvement with seed mortality could be inferred from the experimental conditions: losses because of germination and initial variation in seed viability and seed density were accounted for, no vertebrate or invertebrate seed predators were allowed in the system, experimental units were contained to preclude seed loss from the system, and fertilizer N and corn stover are not known to have a direct graminicidal effect. These logical antecedents suggest that microbial activity was therefore associated with treatment effects on seed mortality in these assays.

Data Analysis. Seed mortality proportion data were subjected to a $\sin^{-1}(x^{0.5})$. transformation (Neter et al. 1996) prior to analysis to remove the artifacts typically associated with analyses of proportion data. The data were then analyzed using the general linear model subroutine of SYSTAT 11.0.1.[5] Models contained terms for replication, run, species, N fertilizer rate, and corn stover addition rate. Cochran's test (Underwood 1997) indicated that variances were homogeneous between runs but not among species; therefore data were analyzed across runs, but within species. Tests of normality and constant error variance indicated that the data met ANOVA assumptions (Neter et al. 1996).

The transformed data set was also used to develop path analysis models of the potential causal relationships between soil fertility and seed fate (Mitchell 2001). Path analysis was performed using the RAMONA subroutine of SYSTAT 11.0.1 on several candidate models including N fertilizer rate, stover rate, soil total inorganic N, soil NO_3–N, soil NH_4–N, soil C:N ratio, germination, seed mortality, and two latent variables. The most parsimonious model was chosen by minimizing Akaike's information criterion (Burnham and Anderson 2002).

Results and Discussion

Soil amendment with 28% UAN and corn stover resulted in a range of soil inorganic N levels, with an order of magnitude difference between lowest and greatest soil total inorganic N at 1 wk after initiation of the bioassay (Table 1). Soil inorganic N was lower in the corn stover–amended treatment, compared to the unamended treatment, at the 0 and 14 ppmw N levels, most likely indicating N

Table 1. Soil amendment effects on soil N parameters at initiation of bioassay.[a]

N addition rate[b]	Corn stover	Soil inorganic N[c,d]	Soil C:N ratio[c,d]
ppm			
0	0	15.9b	11.7a
	3,000	4.9a	12.4b
14	0	35.8d	11.8a
	3,000	21.1c	12.2b
28	0	41.7e	11.7a
	3,000	57.4f	11.5a
SE		2.1	0.13

[a] Abbreviations: N, nitrogen; C, carbon; SE, standard error.
[b] N fertilizer was applied to soil in experimental units in the form of urea ammonium nitrate (28%) at rates equivalent to 0, 14, and 28 ppmw. Finely ground corn stover was applied to soil in experimental units at 0 and 3,000 ppm.
[c] Entries represent means of eight replicate observations.
[d] Within columns, means followed by different lower case letters were found to be statistically different at $P<0.05$ by a protected, Bonferroni-corrected multiple comparison test.

immobilization by the addition of a C-rich substrate (Kuzyakov et al. 2000). This pattern was reversed at the highest N fertilization rate, possibly indicating a priming effect by the N fertilizer (Conde et al. 2005; Kuzyakov et al. 2000) that resulted in rapid mineralization of N from the crop residue. Corn stover C:N ratio was over 50, therefore it would not have rapidly decomposed in soil without substantial additions of N. Soil C:N ratio was greater in the corn stover–amended treatment, compared to the unamended treatment, at the 0 and 14 ppmw N application rates, but did not differ between amendment treatments at the 28 ppmw N rate. Variation in soil C:N levels was narrow, ranging between 11.5 and 12.4. These values of soil C:N ratio fall within a typical range for soils receiving N from fertilizer or organic amendments (Fortuna et al. 2003).

Mean percent seed mortality was low for redroot pigweed (10.9 ± 1.4%), Venice mallow (11.8 ± 2.1%) and giant foxtail (10.9 ± 1.5%), whereas seed mortality was two to three times greater in velvetleaf (24.4 ± 2.8%), giant ragweed (30.6 ± 3.2%), wooly cupgrass (32.2 ± 3.8%), yellow foxtail (30.0 ± 2.7%), and green foxtail (36.1 ± 3.4%) (Figure 1). As would be expected, seed mortality rates were lower for all species for the 2-mo incubation period than rates that were observed for the same species over a 6-mo burial period in a regional study of seed persistence in the soil seedbank (Davis et al. 2005).

Soil amendment treatments affected weed seed mortality for only three of the eight species studied here: velvetleaf, giant ragweed, and wooly cupgrass. There was a significant main effect ($P < 0.05$) of corn stover on velvetleaf seed mortality, with a 40% decrease in mean seed mortality in the stover-amended treatment compared to the unamended treatment. This pattern is consistent with previous observations of limitation of velvetleaf seed mortality in field soil managed with C-rich soil organic amendments compared to soil managed only with synthetic fertilizers (Davis et al. 2006). For both giant ragweed and wooly cupgrass, there was a significant interaction ($P < 0.05$ and $P < 0.01$, respectively) between the effect of N fertilizer and corn stover on seed mortality. Giant ragweed seed mortality was unaffected by stover treatment at the 0 and 14 ppmw N levels ($P > 0.05$ at each N level), but was 64% lower in the stover-amended treatment than the unamended treatment at the 28 ppmw N rate ($P < 0.05$). Wooly cupgrass seed mortality was unaffected by stover treatment at 0 ppmw N, 61% lower in

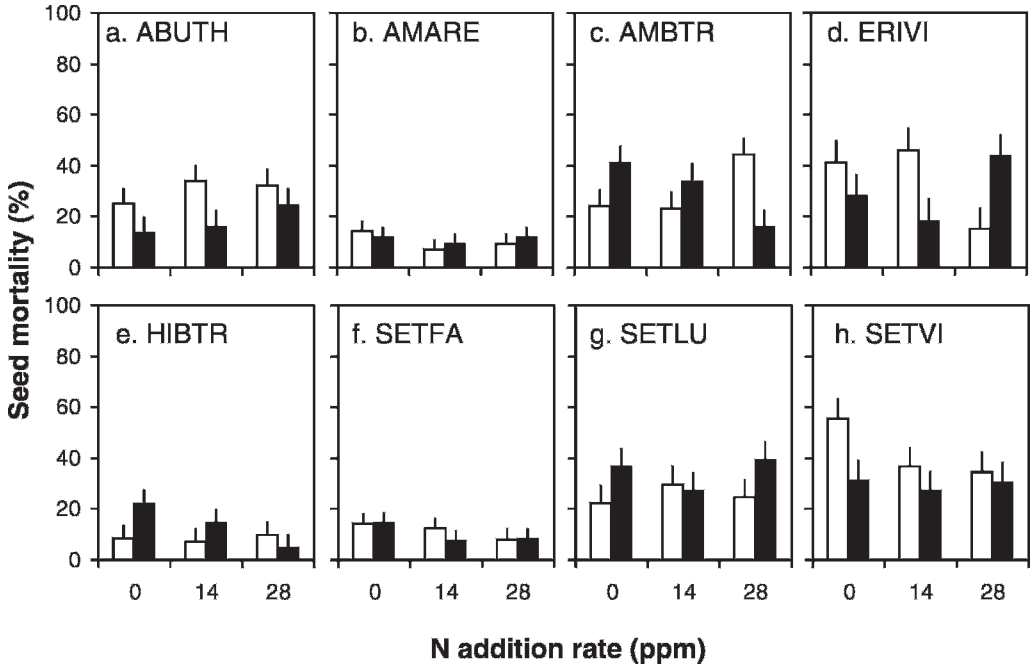

Figure 1. Seed mortality of eight summer annual weed species common to field crop production systems of Illinois. Seeds were incubated for 2 mo in soil amended with varying rates of nitrogen fertilizer and corn stover (open bars = 0 mg stover kg soil^{-1}; shaded bars = 3,000 mg stover kg soil^{-1}). Bars represent the means and standard errors of eight replicate observations. Explanation of five-letter Bayer codes: ABUTH = velvetleaf, AMARE = redroot pigweed, AMBTR = giant ragweed, ERIVI = wooly cupgrass, HIBTR = venice mallow, SETFA = giant foxtail, SETLU = yellow foxtail, SETVI = green foxtail.

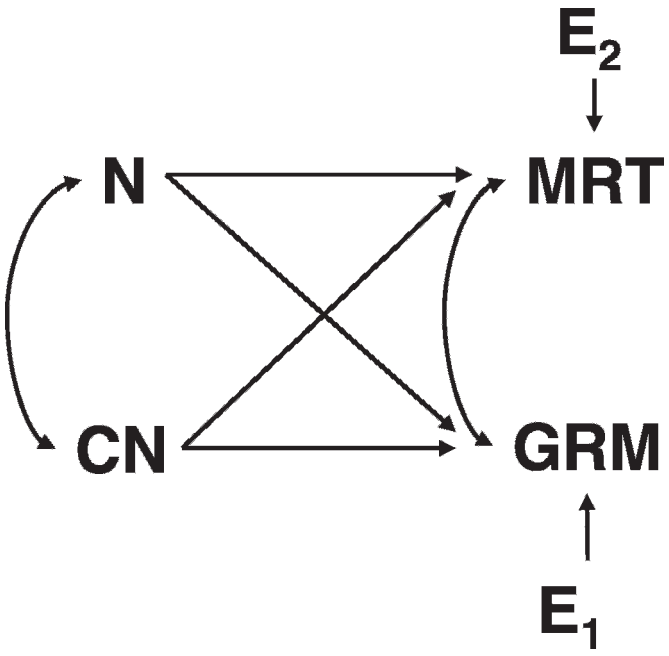

Figure 2. Path analysis model describing potential causal relationships between soil C:N ratio (CN), soil inorganic nitrogen (N), and two latent variables (E_1 and E_2) and $\sin^{-1}(x^{0.5})$-transformed weed seed germination (GRM) and mortality (MRT). See Table 2 for standardized regression and correlation coefficients for the fitted model.

the stover-amended treatment than in the unamended treatment at 14 ppmw N, and 66% lower in the stover-unamended treatment than in the amended treatment at 28 ppmw N. The reversal in the relationship between wooly cupgrass seed mortality in the stover-amended and unamended treatments at the 14 and 28 ppmw N rates offers some evidence that priming of corn stover degradation by the highest fertilizer rate (Conde et al. 2005; Kuzyakov et al. 2000) may have influenced seed fate. The range of N addition rates used in this study was narrow, corresponding to the amount of N that would be applied to a typical rotation crop following corn, such as soybean (0 kg N ha^{-1}) or a small grain (56 kg N ha^{-1}). Had a wider range of N rates been used, simulating a continuous corn scenario, the influence of applied N on seed mortality might have been more pronounced.

Path analysis models were used to address hypotheses 1 and 2 by examining potential causal relationships between the soil parameters and weed seedbank parameters measured here. The most parsimonious model included soil total inorganic N, soil C:N ratio, germination and mortality and two latent variables representing variation unexplained by the model (Figure 2). There was a negative correlation between soil C:N ratio and inorganic N for all species. Velvetleaf had a distinct pattern that contrasted with giant ragweed and wooly cupgrass: there was a positive relationship between soil C:N ratio and seed germination, and a positive relationship between soil inorganic N and seed mortality (Table 2). These results support hypothesis 2: that N fertilizer and stover influenced velvetleaf seed mortality through the direct effect of increasing soil inorganic N, with no effect on seed mortality via germination. Soil that was enriched in N likely favored greater microbial predation of velvetleaf seeds than soil that was enriched in C, supporting the results of Shem-Tov et al (2005) for burning nettle.

Giant ragweed and wooly cupgrass appeared to have related mechanisms behind N fertilizer and stover effects on seed mortality, despite contrasting patterns in how seed mortality of these species responded to experimental treatments (Figure 1). Soil C:N ratio was negatively related to giant ragweed seed germination, which was negatively related to seed mortality (Table 2). Soil inorganic N was positively related to wooly cupgrass germination, which was negatively related to seed mortality. These pathways are related through the inverse relationship between soil C:N ratio and soil inorganic N (Table 2), and support hypothesis 1. For both species, as well as Venice mallow, giant foxtail, and yellow foxtail, soil N parameters appeared to act as a signal to stimulate germination (Egley 1986). For giant ragweed, the signal came from decreasing C:N ratio, whereas for wooly cupgrass, the signal came from soil inorganic N. Increasing germination for both these species resulted in decreasing seed mortality, which was not true for any of the other species in the study. Both giant ragweed and wooly cupgrass have

Table 2. Standardized regression coefficients and correlation coefficients for the path analysis of soil N parameter effects on seed germination and mortality for eight annual weed species.

	Path analysis coefficients							
Bayer code[a]	CN↔N[b]	CN→GRM	N→GRM	CN→MRT	N→MRT	GRM↔MRT	E_1→GRM	E_2→MRT
ABUTH	−0.30*[c]	0.44*	0.16	0.27	0.32*	−0.09	0.90*	0.93*
AMARE	−0.30*	−0.20	−0.01	−0.26	0.01	−0.16	0.98*	0.96*
AMBTR	−0.30*	−0.42*	0.02	0.22	0.07	−0.32*	0.90*	0.95*
ERIVI	−0.30*	0.18	0.44*	−0.16	0.06	−0.33*	0.89*	0.93*
HIBTR	−0.30*	−0.02	0.30*	0.05	−0.20	−0.11	0.95*	0.96*
SETFA	−0.30*	0.17	0.28*	0.06	−0.25	−0.15	0.95*	0.94*
SETLU	−0.30*	0.24	0.41*	−0.05	−0.14	0.02	0.89*	0.98*
SETVI	−0.30*	−0.03	0.08	0.05	−0.03	−0.09	0.98*	0.98*

[a] Explanation of BAYER codes: ABUTH, velvetleaf; AMARE, redroot pigweed; AMBTR, giant ragweed; ERIVI, wooly cupgrass; HIBTR, Venice mallow; SETFA, giant foxtail; SETLU, yellow foxtail; SETVI, green foxtail.

[b] Double-headed arrows denote correlations and single-headed arrows denote standardized regression coefficients, or path coefficients, between variables. Explanation of abbreviations (corresponding to abbreviations in the path analysis diagram shown in Figure 1): C, carbon; N, nitrogen; CN, soil C:N ratio at 1 wk after bioassay initiation; N, soil NO_3–N + NH_4–N at 1 wk after bioassay initiation; GRM, $\sin^{-1}(x^{0.5})$-transformed percent germination; MRT, $\sin^{-1}(x^{0.5})$-transformed percent mortality; E_1 and E_2, error terms 1 and 2, respectively. The correlation between CN and N was the same for all path analyses because a single soil data set was used in relation to the bioassay data for each species.

[c] The symbol * denotes significant correlations or standardized regression coefficients at the $P<0.05$ level.

relatively low persistence in the soil seedbank compared to seeds of many other weed species common to the north-central region of the United States (Davis et al. 2005). Those seeds that do not germinate in a given year appear to be at high risk for seed decay, which is likely to be the result of microbial predation.

For all study species, the effects of latent variables E_1 and E_2 on germination and seed mortality, respectively, had the highest standardized regression coefficients (Table 2). This indicates that other, unmeasured, factors had a greater influence on weed seed mortality than did the independent variables recorded in this study. Although a concerted effort was made to control soil moisture and temperature between experimental units, corn stover addition may have influenced the rate at which experimental units lost moisture on a daily basis. Another important factor may have been fluctuations in quality within a seed lot. Initial seed-lot characterizations were performed on four batches of 50 seeds. Variability in quality among seeds may have been large enough to overwhelm experimental sources of variability. The possibility of such an artifact points to the need for nondestructive means of testing seed viability (e.g., Sawma and Mohler 2003) and other aspects of seed quality so that bioassays may be developed to follow the fate of individual seeds.

There does not appear to be a single, unifying mechanism relating soil N fertility to weed seed mortality that operates across species. Rather, these results suggest that there are three or more types of species-specific mechanisms operating, including (1) no response of seed mortality to soil N and C balance, (2) a response driven indirectly through stimulatory or inhibitory effects of soil N on seed germination, and (3) a response driven through direct effects of soil N on seed decay. Interspecific differences in factors controlling seed persistence in relation to soil properties are likely to have a genetic basis (Gallagher and Fuerst 2005), possibly related to differences in seed coat composition and quality. Seed coats of certain species, such as velvetleaf, contain microbial inhibitors such as phenolic compounds (Kremer 1986). A study of seed longevity of 81 species from the native British flora indicated that seeds with greater concentrations of *ortho*-dihydroxyphenol concentration were more likely to form persistent soil seedbanks, lasting for more than 4 yr (Hendry et al. 1994). Seed age and seed coat integrity may also affect weed seed persistence in soil. Future investigations of weed seed persistence in the soil seedbank should include quantitative information about the initial state of the weed seeds as a covariate for soil and seed fate data.

Sources of Materials

[1] 757 South Dakota seed blower, Seedburo Equipment Company, 1022 W. Jackson Blvd., Chicago, IL 60607.

[2] Model 4 Wiley mill, Thomas Scientific, P.O. Box 99, Swedesboro, NJ 08085 U.S.A.

[3] CE440 CHN combustion analyzer, Exeter Analytical, Inc., 7 Doris Dr., Unit 6A, North Chelmsford, MA 01863.

[4] Conviron 125L incubator, Controlled Environments Limited, 590 Berry Street, Winnipeg, Manitoba, Canada R3H 0R9.

[5] SYSTAT software, 501 Canal Boulevard, Suite C, Richmond, CA 94804.

Acknowledgment

Many thanks to Mr. Deepak Gaur, University of Illinois Crop Sciences undergraduate research assistant, for help in conducting seed mortality bioassays. Mention of trade names or commercial products in this article is solely for the purpose of providing scientific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

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Received August 4, 2006, and approved December 4, 2006.